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**SPECIES RECOGNITION IN GROUND-NESTING
AND HOLE-NESTING DUCKLINGS**

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(Fabricius 1951), and to some extent confirmed (Klopfer 1959), that the young of hole-nesting Wood ducks (*Aix sponsa*) are more able to learn the auditory characteristics of their parent earlier in ontogeny than are surface-nesting Mallard ducklings (*Anas platyrhynchos*), the latter being more able to learn the visual or visual-plus-auditory configurations of the parent (Ramsay and Hess 1954).

Though the above studies shed light on the possible differences in the perceptual learning abilities of hole- and ground-nesting species, they were conducted at a time when it was believed that species recognition in ducklings was primarily a function of learning (imprinting) which occurred soon after hatching and, therefore, these studies did not employ appropriate species-typical auditory and visual stimulation. After these earlier studies (cited above) were completed it was found that imprinting is not requisite to the manifestation of appropriate species identification in domestic chicks or ducklings when species-typical maternal auditory and visual stimulation is employed (Gottlieb 1965a). Specifically, young domestic chicks and ducklings hatched in incubators in the laboratory can identify a hen of their own species without the benefit of previous contact with her and, furthermore, this identification is made primarily on the basis of the maternal call (Gottlieb 1965a, 1966). Consequently, the present study was designed to re-examine the question of the relative significance of auditory and visual perception in relation to species identification in ground- and hole-nesting ducklings, utilizing the species-typical forms of maternal stimulation within each sensory modality.

According to field observations of wild hole- and ground-nesting ducks (Gottlieb 1965b), it would appear that auditory stimulation from the maternal parent is important in both nesting types during the formative stage of the maternal-neonate bond. Specifically, it has been observed that, in both species, vocal interchange between the hen and her young begins before or shortly after hatching and continues until the family leaves the nest about 30 to 48 hours later. These observations, plus the aforementioned laboratory results with domestic ducks and chicks (Gottlieb 1965a, 1966), suggest that auditory perception may be paramount during the early phase of species identification in both Wood ducks and Mallards. Thus, the main difference between the two species may be that in hole-nesting Wood ducklings the motoric ability or tendency has been developed to climb a vertical surface (inside the nest) to approach the maternal call upon leaving the nest, while in ground-nesting Mallard ducklings such

an ability or tendency has not been developed. In other words, the degree of dependence on auditory and visual perception may be the same in both species, but ecological factors may have brought about a selection for the ability to climb a vertical surface in response to the maternal call in one species (Wood duck) but not the other (Mallard).

In view of the foregoing considerations, the current experiments were aimed at assessing the relative importance of species-typical auditory and visual stimulation in the development of species identification during the early postnatal phase in Wood ducklings and Mallard ducklings, while also examining the tendency of these two species to climb a vertical surface in response to their respective maternal calls. Based on the research reviewed above, the alternatives investigated were: (1) that Wood ducklings rely more on auditory perception and Mallards rely more on visual perception; (2) that both species rely more on auditory than visual perception; and (3) that Wood ducklings are more able or inclined than Mallards to climb a vertical surface in response to the maternal call of their species.

EXPERIMENT I

The first experiment consisted of three conditions. The first condition concerned measurement of the following-response of both species of ducklings when they were exposed to a stuffed hen of their own species which emitted a recording of the maternal exodus or leading call (audiovisual condition). These were vocalizations uttered by Wood duck and Mallard hens when they called or led their young from the nest in the field (Gottlieb 1965b). In the second condition the following-response of another sample of Wood and Mallard ducklings was measured in relation to their respective maternal call without the presence of the stuffed hen (auditory condition). And, finally, the following-response of another sample of ducklings from each species was measured in relation to their respective stuffed hen without the presence of the maternal call (visual condition). Thus, the analysis involved the ducklings' response to the audiovisual, auditory, and visual components of a hen of their own species. All the ducklings were incubated, hatched, and brooded in the laboratory and were isolated from maternal stimulation until tested in the experimental apparatus.

METHODS

Subjects. Most of the Mallard eggs were collected from nests at the Dorothea Dix Animal Behavior Field Station in Raleigh, North Caro-

lina, where a population of 40 to 80 free-wing Mallards has been maintained under non-captive conditions since 1962. The original stock of wild Mallards came from the Delta Waterfowl Research Station in Canada in 1961. For comparison other Mallard eggs were obtained from two game farms in Minnesota and the U. S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland.² Upon testing, no behavioral differences existed between these populations. All of the Wood duck eggs come from wild birds which nest in artificial nestboxes at the Dorothea Dix Field Station and a private waterfowl refuge in Raleigh. These nestboxes are attached to poles or trees above or near water, and are of the type widely used throughout the United States. Pictures of the inside and outside of such artificial Wood duck nestboxes are contained in previous publications (Gottlieb 1963, 1965b).

Incubation and Brooding Procedures. The eggs were incubated and hatched in forced draft incubators in the laboratory. The background noise level in the incubators was 71 db (re 0.0002 microbar at 1000 cycles), supplied by a room air conditioner and a fan in the incubator. Upon hatching the birds were visually isolated from each other in a brooder (86-92°F), where the background noise level was maintained at 69-70 db by air conditioners. The incubators and brooders were located in sound-attenuated rooms. The individual cartons in which the birds were kept were not entirely light-proof, so each bird had some limited opportunity to see parts of itself from light leaks in the top of its carton. The birds also had a limited amount of opportunity to hear themselves insofar as their own vocalizations penetrated the background noise levels of the incubators and brooders. The birds were, however, absolutely shielded from any direct contact with maternal stimulation prior to being tested in the experimental apparatus. Nevertheless, for studies like the present one, a methodological difficulty is presented by the fact that auditory inter- and self-stimulation among sibs enhances responsiveness to maternal auditory and visual stimulation in domestic ducks (Gottlieb 1966). The main justification for the present approach is that the opportunity for such pre-testing visual and auditory stimulative factors to influence the results was apparently equal in the incubation and brooding procedure for both species.

Testing Procedure. Within 16 to 30 hours after hatching, each bird was placed in one of three test situations.

1. Audiovisual Test. Nineteen Wood ducklings

² James McGilvrey kindly collected the Mallard eggs supplied by the Patuxent Research Center.

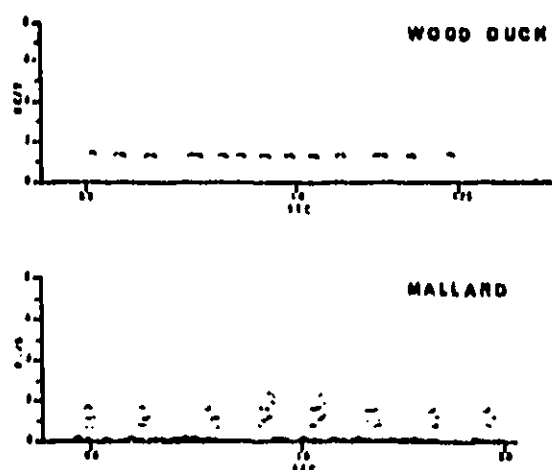


FIG. 1. Narrow-band Sonograms of the Wood duck and Mallard maternal calls used in the experiments. Kilo-cycles per sec (KC/S or KHz) is shown on the ordinate and time (sec) on the abscissa.

and 20 Mallard ducklings were individually exposed for 20 min in the experimental apparatus (Gottlieb 1965a, Fig. 1) to a stuffed hen of their own species. The hens emitted a repetitive recording of the maternal exodus or leading call of the species through a speaker in its underside.

An audio-spectrogram (Sonogram) of each maternal call is shown in Figure 1. Each maternal call was recorded in such a way that it repeated itself approximately every three seconds. The calls were free of background noises such as the cheeping of ducklings. The following-response of the ducklings was measured during a 20-min exposure to the calling model as the model moved about a circular (14 ft circumference) path at the rate of one revolution every 58 seconds, including a 5-second pause after every 20 seconds of movement. The movement and pauses of the model were automatically controlled. The background noise level in the apparatus, produced by an air conditioner, was 61-62 db at the point where the duckling was placed in the apparatus. The intensity of the Wood duck maternal call was 62-65 db and the Mallard maternal call was 62-68 db measured at the ducklings' starting position 6 inches to the rear of the stuffed maternal replica. A temperature of 72-78°F was maintained in the apparatus.

Each duckling did or did not accumulate a "following score" (time in seconds) according to four criteria:

A. A following score was earned if the duckling was within 12 inches to the rear or 4 inches to the side of the replica, with its head oriented toward and its body moving in the same direction as the replica. Scoring began only after the duck-

lings had taken at least 3 steps under these conditions.

B. If the duckling's entire body was in front of the replica, no following score was accumulated.

C. If the duckling was fulfilling the criteria for following prior to a pause of the replica, the duckling continued to accumulate time for following during the pause provided it stayed within 4 inches to the side or rear of the replica. If the duckling had not been following the replica before the pause, but ran over to the replica during the pause, no credit was given until following ensued.

D. Despite the restrictive nature and rigorous application of the above criteria, some ducklings achieved what appeared to be a chance following score of a few seconds during the 20-min exposure period. To rule out chance following, no duckling scoring 10 seconds or less was considered to have followed the replica.

2. *Visual Test.* The Visual Test was carried out in exactly the same way as the Audiovisual Test except the maternal replica did not emit a call as it moved about the apparatus. Nineteen Wood ducklings and 20 Mallard ducklings were exposed for 20 min to visual testing, and their following-response was scored according to the above criteria.

3. *Auditory Test.* To measure the response of 33 Wood ducklings and 20 Mallard ducklings to the maternal call of their species, certain changes were made in the testing and scoring procedure. A circular opaque black cloth wall was interposed between the duckling and a moving box housing a speaker, as shown in Figure 2. Under these conditions, the duckling was required to follow the maternal call emanating from a concealed sound source as the sound source moved around the apparatus at the rate previously described. The db levels of the calls were in the same range as those in the Audiovisual Test. The criteria for following were the same as above except that the appropriately oriented and moving duckling was credited with following when it was within 8½ inches to the side or 12 inches to the rear of the concealed sound source. As can be seen in Figure 2, the ducklings could approach the speaker from only one side in the Auditory Test, while in the Audiovisual and Visual Tests they could follow the replica from either side. To allow comparison with the Audiovisual and Visual tests, the Auditory Test was also 20 min long.

Statistical Analysis. The Chi-Square Test was used to determine the reliability of differences in the proportion of birds which followed in each condition. The Mann-Whitney U-Test was applied to differences in latency and duration of following (time in seconds) between each condi-

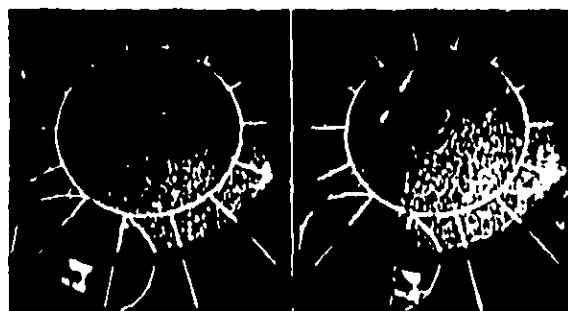


FIG. 2. Mallard duckling is shown as it follows a moving non-visible sound source in the Auditory Test (Experiment 1). A black cloth wall is interposed between the duckling and the sound source. The white lines on the floor of the apparatus are used as guides to determine whether the duckling is tracking the speaker within the distance prescribed for accumulating a following-score. The elliptical white line describes the approach area for a stationary Auditory Approach Test used in experiments other than the present ones. Observations are made through a large mirror (not shown) suspended above the apparatus.

TABLE 1. Following-response of Wood Ducklings and Mallards to the audiovisual, auditory, and visual components of their maternal parent.

	20 Minute Following Test				
	Audiovisual	P _s	Auditory	P	Visual
Wood Ducks (N=72)					
Followed	61%	.07	61%	.001	11%
Av. latency (sec.)	260.7	.007	78.7	.01	171.5
Av. duration (sec.)	750.5	<.0001	79.4	ns ^a	270.0
Mallards (N=40)					
Followed	65%	.001	60%	ns	30%
Av. latency (sec.)	263.3	.07	193.5	.001	561.8
Av. duration (sec.)	410.9	.0003	98.5	ns	127.5

WD showed shorter latency (.06) than Mallards in response to Audio component. No difference between WD and Mallards in response to visual component. WD showed longer duration of following (.02) than Mallards to Audiovisual component.

P_s values represent reliability of differences between adjacent columns. Reliability of differences between Audiovisual and Visual conditions is reported in text.

^a Difference not statistically reliable due to range of variation. Only two birds out of 19 responded in Visual condition and they followed for 11 and 111 sec. each. The standard deviation for Audio condition was 76.1 sec. with 20 out of 33 birds responding.

tion and only included data from birds which had actually accumulated a following score (i.e. non-followers were excluded from these analyses).

RESULTS

The data recorded for each of the three stimulus conditions of Experiment 1 are shown in Table 1. The Wood ducklings showed a stronger response (% followed and latency) to the auditory than to the visual component of their maternal parent, but the Mallard ducklings did not evince a stronger response to the visual component of their parent model relative to the auditory one. In fact, the Mallards responded significantly more promptly to the auditory component than to

the visual one, with no differences in proportion which followed each or duration of following each in the birds which responded.

Ducklings of both species were most responsive in the audiovisual condition as compared with their performances in the other two conditions. The only exception was in the latency of following in the audiovisual vs auditory conditions, in which both the Wood ducklings and Mallards showed a prompter response when exposed to the call without the visual component. However, once the response to the audiovisual stimulus was initiated, the ducklings were able to track it significantly more consistently or easily (duration of following) than the call presented by itself. In comparing the performance of the ducklings in the audiovisual vs. the visual conditions, both species responded more strongly to the audiovisual stimulus on all measures, though some of the differences are of marginal reliability. Specifically, more of the Wood ducklings ($p < .001$) and Mallards ($p < .001$) followed in the audiovisual condition, and they followed more promptly ($p = .10$ and $p = .006$, respectively) and with a greater duration ($p = .06$ and $p = .005$, respectively) than in their respective visual conditions.

In terms of cross comparison between species on the three measures (% followed, latency, and duration), the Wood ducklings bested the Mallards in latency of response in the auditory condition, while there were no differences between species in the proportion which followed or duration of following in the auditory condition. There were no differences between the Wood ducklings and the Mallards in the visual condition—the Wood ducklings responded equally well relative to the Mallards on all three measures. In the audiovisual condition, the Wood ducklings showed a longer duration of following than the Mallards, but there were no differences between species in the percentage which followed or latency of following in the audiovisual condition.

EXPERIMENT II

In Experiment I, 61% of the Wood ducklings responded to the auditory component and 11% to the visual component of their maternal replica. The Mallards showed a statistically unreliable difference (50% vs 30%) in response to the auditory and visual components of their maternal replica, though they showed a much shorter latency of response to the auditory component. Tentatively, it would seem that both species rely relatively more on auditory than visual perception in identifying their parent, with the Wood ducklings showing an even greater reliance on auditory perception than the Mallards.

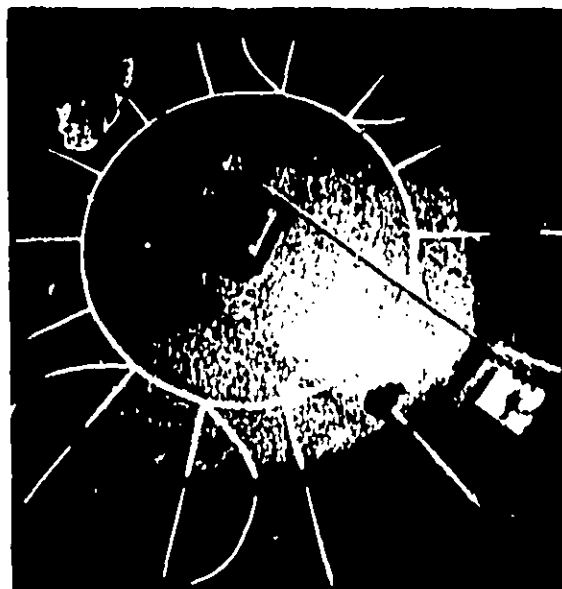


FIG. 3. Mallard duckling following maternal call emanating from a concealed moving sound source in preference to silent visual maternal replica in the auditory vs visual choice test (Experiment II).

To clarify the results of Experiment I, the next experiment involved presentation of the appropriate maternal call and maternal visual replica to ducklings of each species in a simultaneous choice test. In this kind of test, the Wood ducklings should favor their maternal call over the visual replica of their parent, and the behavior of the Mallard duckling should allow a clearer interpretation of their sensory preference.

METHOD

The subjects were 15 Wood ducklings and 20 Mallard ducklings hatched and reared under the conditions of isolation described in Experiment I. At 16 to 30 hr after hatching the ducklings were placed in the apparatus for the visual vs auditory choice test as depicted in Figure 3. The starting positions of the silent visual replica and non-visible speaker were at opposite 90° angles from the point at which the duckling was introduced into the apparatus, and the position of the stimuli was systematically rotated at the start of testing each duckling to exclude the possibility of directional bias.

The ducklings were exposed individually to the moving call and moving visual replica of their own species for 14 min and following time was scored according to the previously described criteria. The speed of movement and pauses of the stimuli were the same as described in connection with Experiment I.

TABLE 2. Response of Wood Ducklings and Mallards in choice test between maternal call and maternal visual replica

	14 Minute Following Test	
	Maternal Call	Maternal Replica
Wood Ducks (N=18)		
Responded.....	83%	0
Av. latency (sec.).....	73.3	—
Av. strength (sec.).....	35.3	—
Mallards (N=20)		
Responded.....	15%	0
Av. latency (sec.).....	87.6	—
Av. strength (sec.).....	66.6	—

No difference between Wood ducklings and Mallards in response to their respective maternal calls.

RESULTS

As can be seen in Table 2, in the simultaneous auditory vs visual choice test ducklings of both species favored the call over the visual representation of their maternal parent. None of the ducklings followed the visual replica at all under these conditions. In addition, there were no differences between the Wood ducklings and Mallards in the incidence, latency, or duration of response to their own maternal call. Despite the relatively prompt response (latency) to the call, neither species accumulated a very high following score (duration). This was due to the fact that the ducklings either lagged behind or, when in close proximity to the call, attempted to jump or climb over the wall to approach the call. In accordance with literal application of the criteria for accumulation of a following score (Method section, Experiment 1), no score was given when the ducklings were jumping or trying to climb the wall even though they were oriented to the call and within 12 inches to the rear or 8½ inches to the side of the call. Though the jumping and climbing behavior was exhibited by both species, it was more pronounced in the Wood ducklings. This behavior also occurred in the auditory condition of Experiment 1, but that test was 20 min long so the birds accumulated a somewhat longer duration of following than in the present 14-min test.

From the standpoint of the purpose of Experiment II, it is important to mention that the birds (both species) did not oscillate between the call and the visual replica as if in a conflict situation, but tended to stay in the general vicinity of the call throughout the test.

EXPERIMENT III

The third experiment was conducted to determine if the ducklings would climb a vertical



FIG. 4. Mallard duckling in Wood duck nestbox (Experiment III). Mallard ducklings were unable to exit from a depth of 12 to 14 inches (left and center photos) in response to their maternal call, but 35% made the exit when the depth was reduced to 4 to 5 inches (right photo). The sound source is in the upper left-hand portion of the photos. The top of the nestbox has been removed for photographic purposes.

cal surface to obtain egress from a nestbox in response to its maternal call emanating from a speaker outside the nestbox. This response tendency is well known in Wood ducklings and is an essential ability for hole-nesting species, while it is not requisite in ground-nesting birds (e.g., Mallards).

Within 16 to 30 hr after hatching, 9 Wood ducklings and 29 Mallard ducklings, hatched and reared under the previously described conditions of isolation, were placed in a Wood duck nestbox inside the experimental apparatus as shown in Figure 4.

The maternal call of their own species emanated from a stationary speaker outside the nestbox (Fig. 4) at the previously described db levels and each duckling was tested individually. The test was continued for five min during which time it was observed whether or not the duckling appeared at the exit of the nestbox. In one condition, the exit was 12 to 14 inches above the sawdust base at the bottom of the nestbox, and in the other condition another group of Mallards was tested when the internal base was raised to within 4 to 5 inches of the exit. The walls on the inside of the nestbox were lined with burlap to allow the ducklings a firm purchase in their ascent to the exit.

In nature healthy Wood ducklings accomplish the exodus from the nest well within four min from the time the parent begins calling from outside (Gottlieb 1963). A very small percentage of Wood ducklings, presumably weak or sickly ones, do not emerge from the nest and they are left behind as the parent leads her brood away from the nesting site. The Wood duck hen apparently stays in the vicinity of the nestbox as long as she hears vocalizations from inside the box, and the ducklings that are left behind either are silent or vocalize at a very low intensity. In contrast to the current experimental conditions,

TABLE 3. Egress of Wood Ducklings and Mallard Ducklings from Wood Duck nestbox in response to their respective maternal call

	Five Minute Test (duckling 12 inches below exit)
Wood Ducks (N=9)	
Appeared at exit hole	89%
Av. latency	100.0 sec.
Mallards (N=18)	
Appeared at exit hole	0%
Av. latency	—
	Five Minute Test (duckling 4 inches below exit)
Mallards (N=11)	
Appeared at exit hole	55%
Av. latency	139.5 sec.

All birds tested individually 15 to 30 hrs after hatching.

in nature the ducklings are exposed to their maternal call for a 30 to 48 hr period prior to the exodus, and they are also stimulated by each other during the exodus. In the present case, the ducklings had not been exposed to their respective maternal calls prior to the test and they were tested singly rather than in groups.

As shown in Table 3, when the internal base of the Wood duck nestbox was at the usual depth from the exit (12 to 14 inches), 8 of the 9 Wood ducklings reached the exit in response to their maternal call within the 5-min duration of the test, while none of the 18 Mallards appeared at the exit under these conditions. The Mallards vocalized infrequently after being placed in the relatively dark nestbox and there was no strikingly audible signs of activity from inside the nestbox when their maternal call came on outside the nestbox. At the end of each test, the lid of the nestbox was gently lifted and most of the Mallard ducklings were observed to be standing quietly at the base of the box and were oriented in the general direction of the call. A greater degree of "distress" calling and activity on the part of the Mallard ducklings had been anticipated.

When the base of the nestbox was raised to within 4 to 5 inches of the exit (Table 3), 55% of the Mallard ducklings made the egress from the box in response to their maternal call. The Mallards' exodus from the modified Wood duck nestbox was not typical of the Wood ducklings' exodus from the unmodified box (above). While the Wood ducklings perched and paused at the exit hole before jumping to the floor below, the Mallards usually went directly from the inside of the box to the floor outside, as if they had jumped out of the box rather than climbed out of it.

Figure 4 shows a Mallard duckling inside the Wood duck nestbox used in the experiment.

DISCUSSION

Relative Importance of Auditory and Visual Perception

The results of Experiments I and II indicate that maternal auditory stimulation plays a potent role in both species as far as attracting the young ducklings to their parent. In neither experiment did the Mallards show a stronger attraction to the visual as contrasted to the auditory component of their maternal stimulus configuration. The results of the auditory vs visual choice test (Exp. II) were especially clearcut in this respect, with all of the Wood ducklings and Mallards which responded showing a unanimous preference for the maternal call and none of the birds following the visual replica of their parent at all under these conditions.

Thus, the hypothesis (Fabricius 1951, Klopfer 1959) that visual stimulation plays a relatively more important role than auditory stimulation with respect to species recognition in ground-nesting species of ducklings was not supported by the outcomes of Experiments I and II. According to these results, during the early post-hatching phase of ontogeny, auditory stimulation from the maternal parent would appear to be relatively more important than visual stimulation in both hole-nesting and ground-nesting ducklings. That this is a matter of relative importance only is attested to by the fact that the combined presence of the auditory and visual components (Audiovisual Test, Experiment I) was most effective in inducing the greatest proportion of birds to follow, as well as inducing the longest duration of following. The fact that the latency of following was swiftest in both species in response to the call presented alone (Auditory Test, Experiment I) is perhaps an indication of the role that the maternal call plays in the early phase of species identification. Namely, the maternal call would seem to function as the selective part of the audiovisual perceptual mechanism for species-recognition, assuring that the approach aspect of the following-response will be prompt and addressed to the biologically appropriate object. For, as Spalding (1873) and many others since his time have shown, the visual perceptual system of young precocial birds is relatively non-specific or non-selective, and when guided by visual perception alone the young bird will approach and follow a wide variety of objects. Naive preferences do exist at hatching in the avian visual perceptual system, e.g., visually naive chicks show prefer-

tial approach or following to particular rates of visual flicker (James 1940), certain colors (Schaefer and Hess 1950, Gray 1961), and forms (Hess 1950). However, these visual preferences are of a rather general nature and would not appear to be capable of narrowing down the hatchling's response exclusively to members of its own species without the participation of visual imprinting. Thus, given the previously demonstrated (Gottlieb 1965a) selective nature of the auditory aspect of the duckling's audiovisual perceptual system for species recognition, visual imprinting can take place in a stable context in each generation.⁴ If both the auditory and the visual aspect of the perceptual system for species recognition were relatively undifferentiated or non-specific, the continuity of the species in each generation would be left entirely to the vicissitudes of imprinting in both sensory modalities, which could be a tenuous affair in species which are highly mobile and active shortly after hatching. In this respect, a further safeguard against the establishment of extra-specific social preferences on the part of the young is evident in the Peking duckling's (*Anas platyrhynchos*) preference for the vocalization of a sibling in a situation where it could follow an extra-specific maternal call or the call of a sibling (Gottlieb 1966). Other experiments in this latter report also indicate the importance of auditory self- and inter-stimulation in hatchlings for facilitating, or perhaps even establishing, the neonate's preference for the maternal call of its own species. Highly developed duck fetuses can both vocalize and hear prior to hatching (Gottlieb 1965c), and this prior auditory self- and inter-stimulation may be the ontogenetic basis for the similarity of sensory (auditory over visual) preferences in Wood ducklings and Mallards. Further experimental analysis of the role of prenatal stimulative factors is required for a full understanding of the sensory preference demonstrated in the present and previous studies. Another question which is prompted by the present results concerns the selectivity of auditory perception in Wood ducks and Mallards. It now needs to be determined whether Wood and Mallard ducklings are equally selective in their

⁴ The concrete fact referred to here and in the previous sentence is that ducklings and chicks can identify the maternal call of their own species without previous direct contact with maternal auditory stimulation (Gottlieb 1965a). Such an ability is apparently not present in the visual sphere and is manifested only after the neonate has actually encountered the visual characteristics of its parent. Both abilities require further ontogenetic analysis to reveal the developmental mechanisms involved, and it would be inadequate simply to label one innate and the other one learned. Some initial progress has been reported on the influence aspect of the problem (Gottlieb 1966).

auditory response to maternal calls of various species.

In the context of the present results, the function of the hen's vocal activity (both species) prior to and during the exodus from the nest under natural conditions can be interpreted in two compatible ways. (1) Given the young's attraction to the maternal call, the hen's vocal behavior can exert a control function which holds the hatchlings in the nest till the exodus, while also serving to promptly draw the young out of the nest during the exodus. (2) Exposure of the young to the particular idiosyncracies of their own hen's call prior to the exodus may establish the basis for individual recognition of the parent which has been observed to be present at the time of the exodus in nature (Gottlieb 1963, p. 90). Along this line, Ramsay (1951 p. 11) concluded from his experiments with several species of older ducklings: "... auditory cues predominate in individual recognition of the parent and ... recognition based on such cues is more exact than that based on form, color, or size." From the comparative point of view, it is interesting that Tschazik (1965) reached a similar conclusion from his field studies of young guillemots (*Uria adae*), while Fischer (1961) found some support for Ramsay's contention in an experimental study of domestic chicks.

Climbing Tendency in Wood Ducklings and Mallards in Response to Their Maternal Call

The results of Experiment III indicate that the Mallards do not manifest the climbing ability of Wood ducklings in obtaining egress from a nest-box in response to their maternal call. Even when the internal base of the nestbox was raised to within 4 to 5 inches of the exit, only 55% of the Mallards obtained egress from the nest.

Therefore, though differences in nest-site ecology were not related to the degree of dependence on auditory and visual perception in these species, such ecological differences were related to differences in motoric tendency (climbing ability) appropriate to the species-typical nesting site. Thus, the most important behavioral difference in the ground- and hole-nesting species of ducklings tested was the manifest ability of the hole-nester in climbing a vertical surface in response to their maternal call and the relative absence or weakness of this tendency in the ground-nesting ducklings.

SUMMARY

The current experiments were aimed at assessing the relative importance of species-typical maternal auditory and visual stimulation in the development of species recognition in the

postnatal phase in Wood ducklings (hole-nesters) and Mallard ducklings (ground-nesters). In addition, the tendency of these 2 species to climb a vertical surface in response to their respective maternal calls was examined.

The experimental findings indicated that maternal auditory stimulation plays a more potent role than maternal visual stimulation in attracting ducklings of both species to their parent. However, the call and the visual replica of the parent presented together induced the strongest following-response in both species, so the maternal call can only be considered relatively more important than the visual characteristics of the parent. According to previous research, the response to visual stimulation is relatively non-specific in naive ducklings and chicks while the response to the maternal call is highly selective in both groups. Therefore, the maternal call would seem to function as the selective part of the audiovisual perceptual mechanism for species-recognition, assuring that the approach aspect of the following-response will be both (1) prompt and (2) addressed to the biologically appropriate object. In this way, visual imprinting can take place in a stable context in each generation, which would not be the case if both the auditory and the visual aspect of the perceptual system for species recognition were relatively undifferentiated.

The similarity in sensory preferences (auditory over visual) in Wood ducklings and Mallards may stem from a similar prenatal sensory background. During the normal course of incubation in the field or laboratory, the birds are exposed to their own self-produced vocalizations both before and after hatching, and it has been previously demonstrated (Gottlieb 1966) that this exposure promotes subsequent responsiveness to the maternal call. This aspect of the problem requires further ontogenetic (prenatal) analysis. Another question which requires study is whether Wood and Mallard ducklings are equally selective in their auditory response.

The main behavioral difference between the Wood ducklings and Mallards tested was the manifest ability of the hole-nesting Wood ducklings to climb a vertical surface in response to

their maternal call and the relative absence or weakness of this tendency in the ground-nesting Mallard ducklings. Therefore, though differences in nest-site ecology were not related to the degree of dependence on auditory and visual perception in these species, such ecological differences were related to differences in motoric tendency (climbing ability) appropriate to the species-typical nesting site.

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DIFFERENCES IN INSECT ABUNDANCE AND DIVERSITY BETWEEN WETTER AND DRIER SITES DURING A TROPICAL DRY SEASON¹

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Abstract. During the dry season in Costa Rica, sweep samples were taken of forest understory insects in three adjacent habitats of increasing moistness (Guanacaste Province; Areas I through III) and in another habitat under a much wetter precipitation regime (Limon Province; Area IV). These samples were then compared with respect to numbers of individuals, numbers of species, size frequencies, weight, developmental stages, species diversity, trophic levels, taxonomic composition and species exclusiveness. The absolute numbers of species increased from Areas I through IV; the numbers of individuals, frequency of small insects, dry weight, individuals per species and percent parasitic species increased from Areas I through III. The several indices of species diversity calculated for the samples only show partial agreement in relative values and trends. The data clearly demonstrate that adjacent tropical communities can have greatly different insect components. The possible effects of the differences between the insect communities of Areas I to III on vertebrate predators and plants are discussed. When compared with temperate data on insect communities there are indications that the four tropical communities examined have a much greater number of species and possibly a greater internal uniqueness than similar temperate communities.

INTRODUCTION

It is common knowledge among entomologists who have collected in the Central American tropics that insect species diversity and composition, and abundance, vary greatly between adjacent habitats and even more so between areas of great differences in the length and intensity of the dry season. This paper is a discussion of such differences between four different habitats during the dry season in lowland Costa Rica. While it is generally acknowledged that a dry season is characteristic of most tropical areas (Allee 1926, Allee and Torvick 1927, Baker and Harrisson 1936, Dobzhansky 1950, Richards 1952, Holttum 1953, Fosberg, Garnier and Kuchler 1961), virtually nothing has been recorded about the influence of a dry season on natural epigaeic insect communities in the New World tropics, nor are observations available on the differences between the insect communities of adjacent habitats (see Beck 1964, Williams 1941, and Rappaport and Najt 1963 for a discussion of soil faunas). Studies in the Old World tropics have been more specific, dealing with the effects of fire (Hocking 1964) or with major pests (e.g., mosquito control, Giglioli 1965, and anti-loeust studies) or have been very general (Owen 1966). Studies of the effect of the dry season on individual insect taxa in the New World tropics are widely scattered. The use of Panamanian forest

plant inflorescences by *Drosophila* as larval substrates clearly shows the negative effect of the dry season on population density (Pipkin, Rodriquez and Leon 1966). A negative effect of the rainy season on tiger beetles (Cicindelidae) can be inferred from the study of Wille and Miehener (1962). The many changes in colony activity and distribution of obligate acacia-ants (*Pseudomyrmex* spp.) during the dry season in Central America are discussed by Janzen (1966a, 1966c). Sexual broods occur soon after the onset of the dry season in some species of army ants (Brown and Schneirla 1950, and included references). Associations of flowering activity with the dry season and large bee populations have been examined, but virtually no hard data on relative bee densities throughout the year are available (Janzen 1966d). Bates (1945) has recorded a negative effect of the dry season on the abundance of some adult mosquitoes in Colombia. Dobzhansky and Pavan (1950) document changes, at times appearing to be associated with the dry season, in the frequency of some *Drosophila* species in Brazil. However, none of the studies cited above provides detailed information on the effect of the dry season on a major part of the insect community of a particular habitat.

This study examines the dry season differences between a dry hillside forest (Area I), an intermediate area (Area II), and the adjacent river-bottom forest (Area III) in the lowlands near

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